THE LIFE HISTORIES OF MARINE PROSOBRANCH GASTROPODS

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INTRODUCTION.

The Australian littoral, especially along its more northerly reaches, displays a diversity and richness of life equal to that of any part of the world. It is still true to say, however, that very little is known of the biology of Australian shore animals. Almost every common species presents problems of numbers, distribution, habits of life and ecological relationships, as well as of such less fashionable matters as comparative anatomy and physiology, each of which calls for intensive treatment if we are to have a full understanding of this conspicuous and colourful component of Australia's natural fauna. The present article calls attention to a small aspect of this vast and complex challenge to our curiosity, a field more neglected than most, and yet among the easiest to gain new information about, life history studies of the littoral representatives of the prosobranch gastropod molluscs.

A full understanding of the opportunities and the scope of the problems in this field demands that account be taken of the present state of our knowledge of prosobranch life histories. Numerous scientific papers have been contributed on the subject by many authors, dating back as far as the middle of the last century, but examination of them, while it yields much that increases our understanding, reveals two important facts. Firstly, it is clear that the numbers of prosobranch species whose life histories are known is greatly exceeded by the number unknown. Generalizations are thus accepted whose factual basis is knowledge of but a fraction of classified genera and species. Secondly, students of prosobranch life histories have made their observations almost exclusively on European and North American species. The species of the southern continents, including Australia, are for the most part different even within families represented in common in both hemispheres, while the southern shores offer further for study numerous tropical and sub-tropical species belonging to families whose life history patterns we know not at all. Since no true picture of any aspect of biology can be gained without encompassing reference to its entire range of manifestation, the significance of this gap in knowledge is plain.

The information that we require of these species can be simply outlined. Onset and duration of the breeding season, the number of fertilized eggs produced by each female, the manner in which the eggs are laid and the nature of the spawn in species where they are not shed freely into the water, details of egg size and yolkiness, the duration of early development and the stage at which the embryo becomes a free-living feeding larva, the form of the larva and its detailed behaviour, the transformation of larva into adult at metamorphosis and the degree to which reorganization takes place, the mortality at each phase of development and the colonisation of the adult habitat by new individuals are all matters which have several kinds of significance. They are an essential part of the record of the natural history of one of Australia's most characteristic groups of animals; a prerequisite to understanding the

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evolution of the prosobranchs; and a basis for analysing ecological relationships among these animals, which cannot be done satisfactorily without knowledge of the mode of maintenance and increase of their populations and the factors which might bring about population movements and limit numbers and geographical range.

It is unfortunate for the intending worker in this field of study, open as much to the amateur as to the professional marine zoologist, that the numerous papers referred to above are scattered through a large number of scientific journals. Furthermore, although the more comprehensive of them review in some detail certain aspects of prosobranch life histories, there is no easily accessible source of reference to contemporary knowledge of the subject such as would quickly guide those wishing to further this knowledge through interest in their own local fauna. It is to fulfil such a need and to juxtapose the known and unknown in terms of specifically Australian opportunities that the present article has been prepared.

A BRIEF SUMMARY OF PRESENT KNOWLEDGE.

The majority of littoral prosobranchs are, of course, dioecious, although hermaphroditism has been occasionally recorded, particularly in *Crepidula fornicata* (Calyptraeidae; Conklin 1897, Orton 1909, 1922, Ankel 1935, 1936, Lebour 1937, Werner 1955). The anatomical differences which allow the prosobranchs to be separated into three systematic orders, the Archaeogastropoda, Mesogastropoda and Neogastropoda*, however, are accompanied by differences in their modes of breeding. Copulation is rare in archaeogastropods except in the Neritidae, the family most closely related to the mesogastropods. Eggs and sperm are either shed freely in large numbers into the water (Text fig. A; Fissurellidae, Haliotidae, Acmaeidae, Patellidae, some Trochidae) or deposited in groups embedded in a simple gelatinous matrix (Text fig. B; other Trochidae, Neritidae). Since in trochids which produce such jelly masses fertilization is external, a form of pseudocopulation involving association in pairs or groups, male and female together, must accompany spawning. Most archaeogastropods produce small microlecithal eggs, 60-100 μ in diameter, which develop rapidly into free-swimming trochophore larvae (Text fig. C) feeding on planktonic micro-organisms. Development of the free swimming larva quickly proceeds to shell formation, 180° torsion and the attainment of the basic prosobranch organization, with head, foot and visceral hump clearly outlined, the foot bearing a thin operculum, the visceral hump being covered by the already spirally coiled shell (Text fig. D). The prototroch of the trochophore becomes greatly enlarged to form the velum, the main propulsive organ of the now completed veliger larva. As planktotrophic life continues, the veliger enlarges and adds further to its shell. Within a short time metamorphosis ensues, the velum is either cast off or resorbed, and the veliger sinks to the bottom and assumes the crawling mode of life of the adult. Successful adoption of the latter depends on settlement on a suitable substratum, but little is yet known of the factors which influence or prevent settling in any species.

Some trochids, neritids and patellids produce larger eggs containing a greater volume of yolk. Here the trochophore organs are largely suppressed and the embryo either becomes free swimming as a lecithotrophic trochophore or remains within the jelly in which it is spawned. In the former case pelagic life is of very short duration, its significance being

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mainly distributive, and settling follows the initial transformation into a veliger with a simple velum, metamorphosis proceeding gradually once the adult habitat is attained. Where such large eggs are spawned in jelly, hatching from the jelly is generally delayed until the completion of metamorphosis, when the embryo emerges as a fully formed crawling miniature adult. One species of acmaeid, *Acmaea rubella*, becomes free at this stage after developing within the maternal oviduct. This is the only known case of viviparity among the archaeogastropods.

The course of development from the egg through to the smallest adult stage may vary between species of a single family, even between species of a single genus, a matter referred to by Coe (1949). The importance of such variations in assisting a taxonomic distinction between closely related species whose adults are almost indistinguishable is being increasingly recognized for marine invertebrates, but does not yet appear to have been exploited in prosobranch systematics save by Anderson (1958), who separates species of *Bembicium* on the basis of differences in their egg masses. Moreover, comparative studies of mode of deposition of the eggs (establishing the environment of early development), egg size and yolkiness, the related degree of development of larval ciliation, speed of development and what might be called the retentiveness of the gelatinous spawn where present (some prosobranch egg masses offer more obstacles to escape of the embryos than others) have received little attention in prosobranchs, although it is obvious that they form an interrelated complex whose total effect broadly determines the life history patterns of species.

Among the mesogastropods, the much larger number of families is associated with a similarly greater diversity of life-history patterns. All of them, however, appear to be derived from the basic pattern of the primitive archaeogastropods.

All mesogastropods show copulation. Subsequently, the female produces eggs that are always yolky and deposited almost always in a cocoon. In the more primitive species this may be simply a gelatinous matrix, as in the archaeogastropods, or a group of such jelly masses together (Text fig. E). The trochophore stage is largely suppressed and passed within the jelly of the cocoon, so that hatching occurs at the earliest as a veliger (Text fig. G). This may be either active planktotrophic (Text fig H), with a long planktonic life, or lecithotrophic, with a short planktonic life (Text fig. I). In the former a well-developed spiral shell of several whorls is formed during growth of the veliger in the plankton; in the latter, the shell is characteristically bulbous and shows little sign of spiral growth before metamorphosis. Metamorphosis is usually a rapid process in the planktotrophic veliger, settling as a miniature adult following it directly, but in the lecithotrotrophic veliger it proceeds gradually after settling has taken place. The same problems of larval settlement and the conditions which influence it exist in the mesogastropods as in the archaeogastropods, as do those of the relationship between mode of spawning, egg size, ciliation, etc. and pattern of the life history.

Great variation occurs in the egg cocoons. In a very few primitive species no cocoon of any kind is produced, the eggs being simply shed freely into the water. Most species produce jelly masses, but there are many which elaborate on this, laying a series of capsules each with a tough outer wall and internal jelly in which the eggs are embedded

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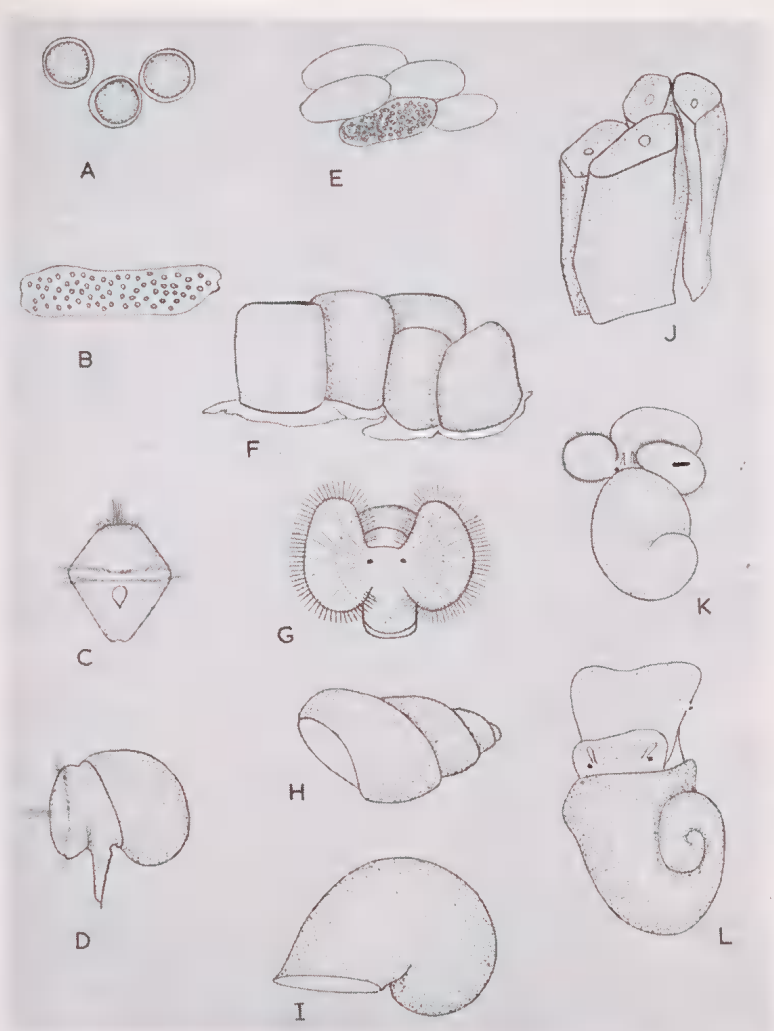
Text figure. (Diagrammatic).

A. Archaeogastropod eggs.
B. Archaeogastropod jelly mass.
C. Archaeogastropod trochophore.
D. Archaeogastropod veliger.
E. Primitive mesogastropod jelly mass (*Bembicium*).
F. Advanced mesogastropod egg capsules (*Mayena*).
G. Mesogastropod early veliger.
H. Shell of planktotrophic late mesogastropod veliger.
I. Shell of lecithotrophic late mesogastropod veliger.
J. Neogastropod egg capsules (*Dicathais*).
K. Encapsulated neogastropod veliger.
L. Neogastropod crawling hatching stage.

(Text fig. F); while the capsules themselves may be deposited in a group of characteristic overall shape. Others lay a tough jelly string with a series of fluid-filled spaces inside, the eggs floating in the fluid, which appears to be a nutritive albuminous substance. In a few species, only one or two of the eggs in each space develop, the others forming nurse eggs which are utilized as food by the developing veligers. These more elaborate provisions for protection and ensured food supply are generally accompanied by suppression of the normal trochophore-veliger temporary organs, more direct development to hatching as a crawling miniature adult, and occasionally the precocious development of the adult feeding apparatus as a means to utilizing available food. Hatching from the spawn is greatly delayed in such species. There appears also to be a correlation between the length of planktonic veliger life and the number of eggs spawned by the female. Species with a long-lived planktotrophic veliger produce eggs in very large numbers: those whose development is direct generally produce many less eggs. A very few species of mesogastropod are ovoviviparous, retaining their eggs within a brood chamber, a specialized part of the oviduct, until their development is completed and they are born as young adults. The European *Littorina saxatilis* is one such species. In fact a clear adaptive relationship between life history pattern and distribution on the shore is seen for the European littorinids, which exhibit a zonation as marked as that of the *Bembicium—Melaraphe—Nodilittorina* zonation of the Australian coast.

L. littorea: lower littoral—eggs laid in floating jelly masses, long planktonic life.

L. obtusata: mid-littoral—eggs laid in jelly masses, hatch crawling.

L. saxatilis: upper littoral—ovoviviparous, born crawling.

L. neritoides: upper littoral—eggs released freely into sea, long planktonic life.

The exceptional life history of *L. neritoides*, which although it is highest on the shore of all these species, shows no obvious adaptation to breeding in such a situation, only emphasises how difficult it is to make generalizations about prosobranch life histories and how great is the need for further information. We do not yet know if comparable adaptations are to be found among the Australian species.

As with the archaeogastropods, the pattern of the life history in mesogastropods may vary within families, even within genera, from the extremes of long pelagic planktotrophic life to direct adoption of the benthic crawling habit. The wide variation that is possible within a single genus is clearly displayed by the example of the littorinids mentioned above. No mesogastropod, however, hatches before the veliger stage.

The neogastropods in general resemble the most specialized of the mesogastropods in their life histories. All of them lay eggs in tough capsules filled with gelatinous fluid (Text fig. J). The eggs may be relatively small, with escape taking place at the veliger stage to a long pelagic planktotrophic life, but usually the eggs are large and yolky, hatching is delayed and pelagic life is either very short or omitted (Text figs. K, L). In some species development within the capsules may take several weeks, hatching occurring as a relatively large juvenile. Nurse eggs are characteristic of certain families of neogastropods, and almost all species provide an albuminous nutriment for the encapsulated

embryos. The problems of relation between mode of oviposition and mode of development, of larval settlement and distribution, etc., are as obvious for the neogastropods as for other prosobranchs, while generic and familial variation again need further detailed study.

In general it can be said that the archaeogastropods tend towards a short pelagic life, the mesogastropods towards a long pelagic life, while in most neogastropods the pelagic phase is omitted. The mesogastropods are thus perhaps the most difficult subjects for life history studies, since even if their egg masses can be found and identified, their planktotrophic veligers are very sensitive to culture conditions, and usually die after a few days. However, in such circumstances a fairly accurate estimate can be made of whether or not the type of veliger under consideration is an important constituent of the plankton by examining:

(a) The numbers of eggs hatching as veligers, which should be high.
(b) The ciliary feeding mechanism of the veliger, which should be conspicuous and elaborate.
(c) The veliger shell, which should be well developed and spirally coiled.
(d) The absence of yolk from the visceral hump and advanced differentiation of the internal organs.

It has been demonstrated from a number of studies of prosobranch life histories that in the colder regions of the northern hemisphere planktonic larvae are either absent or exceptional, but that they become more common among species of the temperate zone, and are almost exclusive among tropical species. Such studies, however, may not reflect the position of the Australian fauna, since they have not included numerous species of neogastropod such as are characteristic in this country. Only detailed investigation of our many unique species can determine whether or not the tentative conclusions that have emerged from studies in the northern hemisphere can be applied without qualification to the Australian littoral prosobranchs.

AN APPROACH TO THE PROBLEM.

Familiarity with the general pattern of life histories to be expected among our littoral prosobranchs, together with a synoptic view of the many aspects of a life history relevant to a complete picture, provide a starting point for the investigation of individual local species. In order to indicate those which would repay study, a summary is given below of the littoral genera which have species commonly represented along various parts of the Australian coast, together with such information as we have about their life histories; and for comparison, species of the same families whose life histories are known, with references to their description, are listed. Of the latter, only species for which a reasonably full account is available are mentioned, and only the important references given for each. These will lead the interested reader to other references and to the few other species of which we have fragmentary knowledge. It is also essential to take account in studies of this kind of the work of Lebour (1937) and Thorson (1946, 1950), whose summaries of the life histories of the prosobranchs of distinct faunal areas, namely, the British prosobranchs and the Danish Baltic prosobranchs, are the only comprehensive accounts of their kind available.

(1) Order *ARCHAEOGASTROPODA.*

Fissurellidae. — Only for one species of this interesting primitive family, *Diodora apertura,* is the life history known (Boutan, 1885), and this species is unusual among primitive archaeogastropods in spawning its eggs in a jelly mass from which the young hatch crawling. Species of *Tugali, Emarginula, Montfortula, Scutus, Elegidion,* etc., would no doubt provide a much broader picture of the life histories of the family.

Haliotidae. — One European species of haliotid, *Haliotis tuberculata,* has been intensively studied (Crofts, 1937, 1955), and one Japanese species, *Haliotis gigantea,* in less detail (Murayama, 1935). Both shed their eggs freely into the water and have a planktotrophic trochophore and veliger. We do not yet know whether this is also true of the Australian species of *Haliotis, Notohaliotis* and *Gena.*

Trochidae. — While three northern hemisphere species of trochid, *Gibbula magnus, G. cineraria* and *G. umbilicalis,* shed their eggs freely and have planktotrophic trochophores and veligers (Robert 1902), all other described species deposit their eggs in jelly and hatch at the crawling stage (*Gibbula tumida* (Gersch 1936), *Calliostoma ziziphynum* and *C. papillosum* (Lebour 1936, Crofts 1955), *Margarites helicinus* (Thorson 1935), *Cantharidus* (= *Trochus*) *exasperatus* and *C.* (= *Trochus*) *striata* (Robert 1902)). Study of the many Australian species included in the genera *Austrocochlea, Trochus, Clanculus, Thaliota,* etc. would greatly extend our knowledge of trochid life histories. *Trochus niloticus* is reported by Moorhouse (1932) to shed its eggs freely in the primitive manner.

Turbinidae. — Nothing appears to be known of turbinid life histories save that the British species *Tricolia pullus* sheds its eggs freely into the water (Lebour 1937). The many common species of Australian genera such as *Turbo, Ninella, Subninella* and *Bellastrea* could serve to establish the typical life history patterns of the family.

Acmaeidae. — The few known species of acmaeid show a wide range of life history patterns. *Patelloida virginea* sheds its eggs freely and has planktotrophic trochophores and veligers (Boutan 1898, 1899). *Patelloida tessulata* (= *Acmaea testudinalis*) lays its eggs in jelly, from which the embryos hatch as pelagic veligers (Wilcox 1905). *Acmaea rubella,* an arctic species, is viviparous (Thorson 1935; see p. 18). Presumably the Australian species of *Notoacmaea, Patelloida,* etc., fit within this pattern, but we do not yet know where.

Patellidae. — All patellids so far studied shed their eggs freely and have planktotrophic trochophores and veliger larvae (*Patella vulgata* (Dodd 1957, Crofts 1955, Smith 1935), *Patella cerulea* (Patton 1886, Lo Bianco 1899), *Patina pellucida* (Crofts 1955, Lebour 1937, Smith 1935)). Artificial fertilization appears to lead to successful culture in this family and could be employed for local species of *Cellana, Patellanax,* etc.

Neritidae. — All neritids so far studied, unlike other archaeogastropods, deposit their eggs in dome-shaped hard capsules. Hatching generally takes place at the crawling stage (*Nerita albicella, N. reticulata,* Risbec 1932) after a long period of development, though in three species of *Nerita* from Bermuda Lebour (1945) suggests that there may be a pelagic phase in the life history. A brackish water species, *Neritina*

fluviatilis, is unusual in having nurse eggs within the capsule, with only a single embryo hatching (Bondensen 1940). Nothing is known of Australian neritid life histories save that the very common *Melanerita melanotragus* produces typical neritid egg capsules (Hedley 1916, 1923).

(2) Order *MESOGASTROPODA.*

Littorinidae. — Reference has already been made (p. 20) to the wide variety of life history patterns shown by the littorinids and to their partial adaptation to environment. The details that have been obtained for northern hemisphere species are summarised below:

(a) Eggs laid singly in floating capsules, hatching as planktotrophic veligers:

Littorina littorea—lower littoral: Hayes (1929), Linke (1934), Lebour (1937), Moore (1937).

L. neritoides—supra-littoral fringe: Lebour (1935b).

L. zigzag ⎫
Tectarius muricatus ⎬ Lebour (1945).
Echinella trochiformis ⎭

(b) Eggs laid in jelly, hatching as planktotrophic veligers.

Lacuna divaricata: Hertling and Ankel (1927).
                     Hertling (1928, 1931), Lebour (1937).

(c) Eggs laid in jelly, hatching at crawling stage.

Littorina obtusata—mid-littoral: Pelseneer (1911), Delsman (1914), Linke (1934).

Lacuna pallidula: Hertling and Ankel (1927), Lebour (1937), Gallien and Larambergue (1938).

(d) Ovoviviparous, young born as planktotrophic veligers.

Littorina angulifera—supra-littoral, mangrove swamps: Lebour (1945).

(e) Ovoviviparous, young born at crawling stage.

L. saxatilis—upper littoral: Pelseneer (1911), Delsman (1914), Linke (1934).

As already pointed out (p. 20), we do not yet know whether the Australian littorinids show corresponding adaptations of the life history to environment, an especially interesting case being the *Bembicium, Melaraphe, Nodilittorina* zonation familiar to all students of rock platform prosobranchs. This group of animals calls for close attention.

Planaxidae. — Nothing is known of planaxid life histories. Species of several local genera, notably *Hinea* and *Planaxis,* could easily be studied.

Rissoidae. — Lebour (1937) points out that the numerous species of small snails included in the Rissoidae probably make an important contribution to the plankton of British waters, and the same may be true of Australian waters, since many rissoid species abound along our coasts. Again, however, we know nothing of their life histories, and indeed only a few are known within the entire family. They characteristically produce oval, tough, thick-walled egg capsules, each containing a small number of eggs (*Onoba semicostata, Alvania punctura, Rissoa sarsi, R. inconspicua,* Lebour (1934a, 1935, 1937)). The three last named species hatch as planktotrophic veligers: the first hatches at the crawling stage.

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Cerithiidae. — The opportunity to extend our knowledge of the life histories of cerithiid prosobranchs lies with the coral reef genera of the north, notably *Cerithium*. The need for such study is shown by the fact that only two cerithiids have been briefly examined so far, the Haiwaian *Clava obeliscus* (Ostergaard 1950) and the Bermudan *Cerithium ferruginum* (Lebour 1945), both of which lay long coiled gelatinous egg strings from which hatch planktotrophic veligers.

Potamididae. — Of this family, closely related to the cerithiids, we have even less knowledge. Only one species, *Bittium reticulatum*, has been adequately studied (Lebour 1936) and found to lay its eggs in a jelly mass from which again hatch planktotrophic veligers. The very common *Pyrazus* and *Bittium* species of Australia could thus be studied to advantage.

Turritellidae. — The turritellids again are almost unknown. Only the life history of *Turitella communis* has been recorded (Lebour 1933a), its eggs being laid in a jelly mass from which lecithotrophic veligers with a short pelagic life emerge. The common turritellids of Australia, e.g., *Turritella* and *Gazameda* species, have not been examined.

Scalidae. — The life histories of two species of *Scala* are known (Vestergaard 1935, Lebour 1937), their eggs being laid in small capsules and probably hatching as planktotrophic veligers. Further, one of these species, *S. clathrus*, is reported to be a protandrous hermaphrodite (Ankel 1936, 1938). Although they are not especially common as Australian littoral forms, scalid species do occur, and may well provide interesting additions to this fragmentary story.

Strombidae. — Like the cerithiids, strombs are characteristic reef animals, yet we know little of their life histories. Ostergaard (1950) and Risbec (1932) report that *Strombus maculatus*, *S. rugosus* and *Lambis* (= *Pterocera*) *lambis* all lay long, fine, coiled gelatinous egg strings, somewhat like those of opisthobranchs, and that the eggs of *S. rugosus* hatch as pelagic veligers. The Australian reef species have not been studied.

Naticidae. — All naticids appear to produce a characteristic spawn, a cylindrical ribbon of jelly covered externally by sand grains and having inside large individual egg spaces filled with nutritive albumen. The life histories of three northern hemisphere species have been studied, and show a wide range of variation. *Natica nitida* (Hertling 1932, Lebour 1937) hatches as a planktotrophic veliger, *N. pallida* (Thorson 1935) hatches at the crawling stage and *N. catena* (Ankel 1930), (Hertling 1932) hatches again at the crawling stage after a long period during which it feeds on nurse eggs. How far the life histories of Australian species of *Conuber* (= *Uber*), *Natica* and *Mamilla* correspond to any of these types is unknown.

Cypraeidae. — Although the cypraeids are among the best known of Pacific prosobranchs, astonishingly little is known of their life histories and nothing at all for Australian species. Ostergaard (1950) describes the early stages of five Haiwaian species of *Cypraea*, all of which lay numerous small horny capsules from which hatch planktotrophic veligers, and records instances of brood protection on the part of the females. Lebour (1932) describes similar capsules and veligers for *Simnia patula* and (1937) mentions that brood protection and small horny capsules are typical of the family.

Lamellariidae. — Only a few lamellariid species are recorded for Australia, and little is known of them, but any of them would repay further examination as to their life histories, for such information as we have on this family shows it to have a unique pattern of development involving planktotrophic veligers characterised by an additional larval shell, presumably flotatory in function, known as echinospiras. Furthermore, the eggs are laid in capsules within holes bored in the tests of compound ascidians by the spawning female. Such a life history pattern has been recorded for *Lamellaria conspicua* (Ankel 1935, Lebour 1935a) and *Trivia europea* (Pelseneer 1926, Lebour 1931b), and is probably followed by *Velutina velutina* (Lebour 1935, 1937).

Cassidae. — Nothing is known of cassid life histories. As with cerithiids, the common Australian species of *Cassia, Xenogalea* and *Phallium*, etc., provide a unique opportunity to fill this gap.

Cymatiidae. — Many well-known species of symatid occur on the Australian coast, belonging to such genera as *Charonia, Monoplex, Cymatilesta* and *Mayena*. The life history of *Cymatilesta spengleri* has been described (Anderson 1959), the eggs being laid in an elaborate group of capsules from which hatching occurs at the crawling stage; but no other life history within the family is known. Variations in the life history patterns of different species must be considerable, however, and deserve further study, since Lebour (1945) records planktotrophic veligers for two species of *Cymatium* from Bermuda.

(3) Order *NEOGASTROPODA*.

Buccinidae. — Life histories are recorded for three species of buccinid, *Pallia tincta* (Lebour 1945), *Sipho sp.* (Thorson 1935) and *Buccinum undatum* (Portmann 1925, 1926, 1927, 1930, Lebour 1937). All lay their eggs in tough capsules and are typified by many nurse eggs and the hatching of a few young at the crawling stage. It would be interesting to know whether the Australian species of *Cantharus, Cominella*, etc., confirm this as the typical pattern.

Nassariidae. — Like the buccinids, the nassariids appear to show a single life history pattern characteristic of the family, producing horny, tough, bottle shaped capsules from which the young hatch as planktotrophic veligers. This has been found for *Nassarius reticulatus* (Pelseneer 1911, Ankel 1929, Lebour 1931a, 1937), *N. pygmaeus* (Vestergaard 1935) and *N. incrassatus* (Lebour 1931a). We do not yet know if it is true for Australian species of *Nassarius, Parcanassa*, etc.

Fasciolariidae. — Very little is known of fasciolariid life histories. Portmann (1955) provides a little on *Fusus*, while Allen (1950) briefly refers to the Australian species *Pleuropoca australasia*, which lays its eggs in bell-shaped capsules from which the young, after a cannibalistic existence, hatch at the crawling stage. We need to know much more of species of such genera as *Colus* and *Peristemia*.

Galeolidae. — One of the largest of all prosobranchs, *Megalotractus aruanus*, graces the Australian shore as a member of this family. Allén (1950) describes the complex egg capsules of this species, from which the young hatch at the crawling stage, but we do not yet know the details of its development or of that of any other galeolid save *Fulgur*, described by Conklin (1907), with a life history pattern similar to that of *Megalotractus*.

Muricidae. — The life histories of several species of muricid have been described. All lay their eggs in vase-shaped capsules, from which the young hatch at the crawling stage (*Trophon muricatus* (Lebour 1936), *T. clathratus* (Thorson 1940), *Murex blainvillei* (Franc 1948), *Urosalpinx cinerea* (Lebour 1937), *Nucella lapillus* (Pelseneer 1911, Portmann 1925, 1926, 1930, Lebour 1937), *Neptunea antiqua* (Thorson 1935, 1941)), while in the two last-named species the young consume numerous nurse eggs before hatching. *Bedeva* (= *Trophon*) *hanleyi* is the only Australian species whose life history is known (Hedley 1916), and it resembles those species above which lack nurse eggs. Much remains to be learnt of species of *Chicoreus, Acupurpura, Murex, Agnewia*, etc., on Australian shores.

Mitridae. — Species of mitre shell remain common yet unstudied, in such genera as *Vexillum, Strigatella* and *Vicimitra*. The only information on life histories in this family is provided by Ostergaard (1950), who states for *Mitra astricta* and *M. auriculoides* that the eggs are laid in vase-shaped capsules and the young hatch as late veligers, probably briefly pelagic.

Conidae. — The many species of cone common on Australian shores again have unknown life histories. A few species have been briefly studied in other countries by Ostergaard (1950), Lebour (1945), Thorson (1940) and Risbec (1932). All lay their eggs in flattened egg pouches, but while the majority hatch as planktotrophic veligers, at least one species, *Conus omaria*, hatches at the crawling stage.

Turridae. — In this family, as in the cones and mitres, many species occur and none have been studied. We have some information from the work of Vestergaard (1935) and Thorson (1935) to show that some species of *Bela* hatch crawling, while Lebour (1933b, 1934b, 1937) has shown that species of *Philbertea* and *Mangelia* have planktotrophic veligers. Eggs always appear to be laid in lens-shaped capsules.

Volutidae. — Volutes are numerous on Australian shores, and in other parts of the world, yet only one species has been investigated as to its life history. This is the well-known Australian Baler shell, *Melo umbilicata*, which is described by Allen and Middleton (1946) as producing a complex mass of egg capsules from which the young hatch crawling at a late stage of development. As with the cones and so many other families, there are numerous problems of distribution and systematics in the volutes which require as an aid to their solution a detailed knowledge of life histories.

For the rest, the Thaididae (*Mancinella, Dicathais, Morula*, etc.), Magilidae (*Rapa, Magilus*, etc.), Harpidae (*Harpa*, etc.), Oliviidae (*Oliva* spp.), Marginellidae (*Marginella* spp.) and Terebridae (*Terebra*, etc.), not only is there no recorded knowledge of the life histories of Australian species, but there is no information as to the life history patterns of any species. Among these completely unknown families and among those for which we have an amount of information that, as shown above, is small at best, the problems outlined in the introduction stand out strikingly. No one worker can possibly solve them all. It can only be hoped that all those whose interests lie among molluscs will see fit to add where they can to this fascinating and biologically important story.

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